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An Examination of the Seeds of some Native Orchids.

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(Plates CL.–CLII.)

During the past year some research has been made, at the suggestion of Dr. Britton, on the seeds of the North American Orchids to determine their structure and to note what additional characters of classification and relationship the seeds themselves might afford.

The seeds are membranous, rather elongated capsules, loosely embracing an elliptical, ovate or pyriform nucellus. In organization they indicate a low type of flowering plant. The nucellus is composed of a large number of polyhedral cells, which are filled with a granular, amber-colored mass, imbedded in which is a great abundance of oily matter. The embryo is exalbuminous, and no cotyledon and radicle are formed. The Orchid seeds, therefore, are of interest as furnishing an example of the arrested stage of embryonic development. With germination the cells of the nucellus divide, and eventually form tuber-like buds that ultimately give rise to the plant. In this peculiarity the Orchid resembles many saprophytes. Especially in the structure and outward appearance of its seed does it closely resemble those of several Ericaceæ, particularly *Monotropa*. The nucellus is generally an excellent illustration of the geometrical arrangement of cells in vegetable growth. Two or more confocal periclines are associated with a usually larger number of orthogonal hyperbolic trajectories. See *Pogonia ophioglossoides* (and fig. 17, Plate CLI.).

Surrounding the nucellus is the integument. Before fertilization it presents the usual form as seen in the ovules of other plants, but after fertilization it develops rapidly, assuming an inflated sac-like form, and in the majority of species greatly exceeds the nucellus in its growth. The seeds are anatropous and sessile; and when removed from the placenta the location of the hilum is marked by an opening. This is caused by the shrinking or, possibly, by the partial absorption of the chalaza, remains of which may still be seen in the ripened seed. This leaves the integument alone connected with the placenta. The free ends, therefore, lend to the seeds the appearance of an arillus, the opening at what seems to be the apex being due to the bending in of the cells of the inflated integument as they approach the hilum. The testa is the conspicuous feature of the seed, and with the embryo furnishes one of the family features or distinguishing characters of the order. It is composed of cells of varying forms, as seen in the plates. The outer margins of the cell wall are much thickened. Thus the testa presents in its outward aspect a ribbed surface, and gives to the seed a cage-like appearance. In *Pogonia ophioglossoides* the so-called ribs (thickenings) do not correspond to the cell divisions, but form long bands over the length of the testa, branching and running together somewhat at either extremity, (fig. 19, Plate CLII.). The sides of the cells, as well as all the other margins, are extremely delicate and colorless. The inner face of the cell often receives an elegant sculpturing from delicate bands that are quite characteristic of the several species in which they occur. These lines are noticeably stronger towards the base of the testa in some species, quite fading out at the apex. This faulty development of the nucellus together with the delicacy of the seed coat is doubtless the cause of the relative scarcity of Orchids. Remembering the large number of pods usually produced by each plant and that each pod contains something like six thousand seeds, we realize the enormous fatality among the seeds. This is not in any way connected with a lack of fertilization. The classical work of Darwin has demonstrated the completeness of this process, were it necessary to go back to the flower to ascertain the fact. The whole appearance of the seed is that of a waif, poorly developed and insufficiently

protected to retain its vitality, in the extremes of our climate. It would appear that the seed is not in surroundings congenial to its nature, and has not yet been able to adapt itself to its environment. This also doubtless explains the paucity of species found in the Northern United States. The seeds are beautiful objects under the microscope. Elegant in outline their beauty is enhanced by the graceful curves of the cell-margins, which often wind into fantastic figures, or build up the testa with cells of mathematical exactness. The clearness of the cell wall in some species (*Listera cordata*) reminds one of the valves of a diatom, while a study of the delicate markings on the inner surface of the cell, tax not a little the patience and skill of the microscopist.

I have been greatly interested in the examination of specimens of the so-called Vanilla Bean, gathered in various parts of the world. The value of these pods varies greatly, dependent upon the locality in which they grow. So close is their resemblance, however, that the merchants have great difficulty in distinguishing them. The testa is very thick and strong. Instead of a ribbed surface the whole outer wall, save a slit-like central portion, is evenly thickened and forms a heavy plate. Save in this particular and their dark reddish brown color, the seeds are identical in structure with those of our native orchids. The resemblance of the eight specimens examined is very close. With perhaps two exceptions, the seeds would appear to belong to the same species. In the other specimens some variations were noticeable, probably due to climate. The constancy of these features as a basis of distinguishing them would necessitate a wider comparison than I have been able to make.

In examining the seeds of our Eastern orchids examples were chosen in each case that as far as possible would be typical of the species. The estimates are made upon normally developed seeds, which were not distorted by luxuriant growth or dwarfed by untoward circumstances. I believe that a wider study of the forms will make no material change in the data presented. In all possible cases comparison of fruit from widely separate localities has been made, and with rare occurrence has marked variation of the seed been manifest. Occasionally the sculpturing of the cell-wall changes, and often the variation of the cell dimensions is consid-

erable, so that the values given in the measurements of the cells, which are the averages of the cells taken from base to apex of about twenty specimens in every case, cannot be found applicable to all cases, but I trust that the proportion which these figures form will be found to be very constant. Such has been the experience in all cases examined. Furthermore, it should be said that having selected as carefully as possible a seed that illustrated most fully the characters of its species, it was drawn as it actually existed. No attempt has been made to introduce into the drawings the salient points of the species that were not already present. So that while some features may not be well brought out I judge that this course will result in a truer representation of the seeds and in less liability to error.

Looking at the seeds as a whole, a unity of form, structure, and organization appear as constant features of family relationship. A comparison of the seeds, however, reveals wide variation and establishes relationship as told by the seeds themselves widely differing from that of the Manuals of Botany. In some instances the relative positions of genera remained unchanged. More often not only does a misplacement of genera seem manifest, but a total disarrangement of tribal relations results. By a comparison of the figures and their explanations the natural relationship of the species as based upon the seed characters at once becomes apparent. Two extreme types are manifest; the one characterized by its elongated tapering testa and elongated cells. Of this *Tipularia* is the type, to which stand related more or less closely, as is shown by the plates, *Aplectrum* and *Calypso*, *Gyrostachys* and *Peramium*, *Cypripedium*, *Pogonia* and *Orchis*. The opposing type is characterized by obovoid or inflated testæ and shorter cells often equilateral. Of this *Corallorhiza* or *Hexalectris* may be taken as the type, and as related would appear *Listera*, *Achroanthes* and *Liparis*, *Habenaria*, *Arethusa* and *Epipactis* and *Limodorum*.

The genera have been taken up in the sequence followed in the Sixth Edition of Dr. Asa Gray's Manual of Botany, of the Northern United States.

I. ACHROANTHES, Raf.

Achroanthes unifolia (Michx.) Raf. (*Microstylis ophioglossoides*, Nutt.) Testa obovoid, about twice as long as thick, averaging

0.343 × 0.19 mm. Cells irregularly polygonal, becoming longer and narrower toward the summit, about twice as long as wide, averaging 0.047 × 0.022 mm. (Plate CL., figs. 1, 1a.)

2. LIPARIS, Richard.

Liparis liliifolia (L.) Richard. Testa oblong, slightly narrowed at base, about three times as long as thick, averaging 0.35 × 0.12 mm. Cells regular, oblong, about three times as long as wide, averaging 0.05 × 0.017 mm. (Plate CL., fig. 2.)

3. CALYPSO, Salisb.

Calypso bulbosa (L.) Reichenb. (*Calypso borealis*, Salisb.) Testa oblong, tapering towards apex, about five times as long as thick, averaging 0.59 × 0.125 mm. Cells regular, oblong, averaging 0.085 × 0.025 mm., thus over three times as long as broad. Inner cell wall finely reticulated. (Plate CL., figs. 3, 3 a.)

4. TIPULARIA, Nutt.

Tipularia unifolia (Muhl.) B. S. P. (*Tipularia discolor*, Nutt.) Testa oblong, acute, about four and a half times as long as thick, averaging 0.534 × 0.121 mm. Cells regular, oblong, about ten times as long as wide, averaging 0.15 × 0.015 mm. Inner cell wall closely, at times loosely reticulated. (Plate CL., figs. 4, 4 a.)

5. APLECTRUM, Nutt.

Aplectrum spicatum (Walt.) B. S. P. (*Aplectrum hiemale*, Nutt.) Testa fusiform, about nine times as long as thick, averaging 1.36 × 0.153 mm. Cells irregularly oblong, about eight times as long as wide, averaging 0.125 × 0.0168 mm. Inner cell wall banded with delicate parallel or branching lines. (Plate CL., figs. 5, 5 a.)

6. CORALLORHIZA, Haller.

Corallorhiza innata, R. Br. Testa obovoid, about twice as long as thick, averaging 0.48 × 0.23 mm. Cells oblong, becoming polygonal at the apex, about twice as long as wide, averaging 0.069 × 0.037 mm. Inner cell-walls sparsely banded, lines very irregular and obscure. (Plate CL., figs. 6, 6a.)

Corallorhiza multiflora, Nutt. Testa oblong-obovoid, about five times as long as thick, averaging 0.70 × 0.172 mm. Cells longer and narrower than in innata, about three times as long as wide, averaging 0.065 × 0.021 mm. Inner cell-wall banded with parallel sometimes anastomosing or branching lines. (Plate CL., figs. 7, 7a.)

7. HEXALECTRIS, Raf.

Hexalectris aphyllus, Raf. Testa elliptical, obtuse, about twice as long as thick, averaging 0.485 × 0.221 mm. Cells elongated, becoming polygonal towards apex, about three times as long as wide, averaging 0.065 × 0.0196 mm. Inner cell wall marked by excessively branching lines. (Plate CLI., figs. 8, 8a.)

7A. BLETIA, R. P.

Bletia verecunda, Sw. Testa obovoid, about one and a half times as long as thick, averaging 0.231 × 0.171 mm. Cells polygonal, about one and a half times as long as broad, averaging 0.061 × 0.041 mm. Added for comparison with *Hexalectris.* (Plate CLI., fig. 9.)

8. LISTERA, R. Br.

Listera cordata (L.) R. Br. Testa oblong-fusiform, about three and one-half times as long as thick, averaging 0.845 × 0.25 mm. Cells square or polygonal, about one and a half times as long as wide, averaging 0.032 × 0.025 mm. (Plate CLI., fig. 10.)

Listera australis, Lindl. Testa subrotund, about one and a half times as long as thick, averaging 0.362 × 0.20 mm. Cells polygonal, rather longer than broad, averaging 0.036 × 0.028 mm. (Plate CLI., fig. 11.)

Listera convallarioides (Sw.) Nutt. Testa obovoid, about twice as long as thick, averaging 0.412 × 0.207 mm. Cells polygonal, somewhat longer than broad, averaging 0.034 × 0.026 mm. (Plate CLI., fig. 12.)

9. GYROSTACHYS, Persoon.

Gyrostachys cernua (L.) Kuntze. (*Spiranthes cernua*, Richard.) Testa oblong, contracted towards apex, over four times longer than thick, averaging 0.541 × 0.112 mm. Cells regular, oblong, shorter towards apex, about seven times longer than wide, averaging 0.132 × 0.019 mm. Inner cell wall marked by delicate, parallel, subdistant lines. (Plate CLI., figs. 13, 13a.)

10. PERAMIUM, Salisbury.

Peramium repens (L.) Salisb. (*Goodyera repens*, R. Br.). Testa elongated, slightly fusiform, about seven times longer than thick, averaging 0.877 × 0.123 mm. Cells square to oblong, somewhat irregular, about three times longer than broad, averaging 0.052 × 0.019 mm. (Plate CLI., fig. 14.)

Peramium pubescens (L.) (*Goodyera pubescens*, R. Br.). Testa elongated, tapering towards apex, about ten times longer than thick, averaging 0.91 × 0.084 mm. Cells regular, elongated, about eight and a half times longer than broad, averaging 0.121 × 0.014 mm. (Plate CLI., fig. 15.)

11. EPIPACTIS, Hoff.

Epipactis viridiflora (Hoff.) Reich. (*E. Helleborine*, var. *viridens*, A. Gray). Testa elongated, somewhat fusiform, about five times longer than thick, averaging 1.31 × 0.261 mm. Cells polygonal, becoming hexagonal towards base, about twice as long as broad, averaging 0.048 × 0.018 mm. (Plate CLI., figs. 16 and 16a.)

12. ARETHUSA, L.

Arethusa bulbosa, L. Testa oblong, less than twice as long as thick, averaging 0.45 × 0.243 mm. Cells oblong to square, smaller towards base, over twice as long as wide, averaging 0.0425 × 0.0171 mm. (Plates CLI. CLII., figs. 17a and 17.)

13. LIMODORUM, L.

Limodorum tuberosum, L. (*Calopogon pulchellus*, R. Br.) Testa oblong, tapering at apex and base, about three times as long as thick, averaging 0.723 × 0.207 mm. Cells regular, oblong, about two and a half times as long as wide, averaging 0.033 × 0.014 mm. (Plate CLII., fig. 18.)

14. POGONIA, Juss.

Pogonia ophioglossoides (L.) Ker. Testa oblong, tapering at apex, ribbed by longitudinal bands that branch at base and apex, about seven times as long as thick, averaging 1.23 × 0.183 mm. Cells oblong, hexagonal, about three times longer than wide, averaging 0.0946 × 0.0298 mm. Inner cell wall banded by delicate lines that usually fade out above nucellus. (Plate CLII., figs. 19, 19 a.)

Pogonia trianthophorus (Sw.) B. S. P. (*Pogonia pendula*, Lindl.) Testa oblong, about as long as thick, averaging 0.570 × 0.197 mm. Cells oblong or polygonal, about two and a half times longer than wide, averaging 0.0525 × 0.0226 mm. Inner cell wall banded with branching, irregular, sub-distant lines. A variable form, sometimes longer and narrower, or with inflated summit and contracted base, having little in common with the seeds of the species of Eupogonia. (Plate CLII., figs. 20, 20 a.)

Pogonia verticillata (Willd.) Nutt. Testa oblong, about six times longer than thick, averaging 1.16 × 0.176 mm. Cells oblong, about five times longer than broad, averaging 0.110 × 0.0236 mm. (Plate CLII., fig. 21.)

Pogonia affinis, Austin. Testa oblong, about six and a half times longer than thick, averaging 1.183 × 0.170 mm. Cells oblong, about five times longer than broad, averaging 0.117 × 0.0255 mm. (Plate CLII., fig. 22.)

15. Orchis, L.

Orchis spectabilis, L. Testa oblong, slightly tapering at ends, about four and a half times longer than thick, averaging 0.57 × 0.12 mm. Cells regular, oblong, about five times longer than wide, averaging 0.117 × 0.022 mm. (Plate CLII., fig. 23.)

16. Habenaria, Willd.

Habenaria ciliaris (L.) R. Br. Testa oblong, about two and a half times as long as thick, averaging 0.452 × 0.18 mm. Cells oblong or polyhedral, about three times longer than wide, averaging 0.0496 × 0.0157 mm. (Plate CLII., fig. 24.)

17. Cypripedium, L.

Cypripedium pubescens, Willd. Testa elongated-fusiform, about five times as long as thick, averaging 1.35 × 0.25 mm. Cells oblong, about five times longer than wide, averaging 0.14 × 0.023 mm. (Plate CLII., figs. 25, 25a.)

In determining species the seeds are not an uncertain element. While it would not be possible to take any one seed, and from it alone locate its position, not a collection of seeds from any fruit has failed to indicate such pronounced individual characters as to render a confusion of species possible. Consider, for example, such troublesome species as *Peramium repens* and *P. pubescens*. While the generic features are pronounced in all the seeds, in each species is apparent certain individual characters that sharply separate them. The more graceful proportions and nicer fitting of cells, together with their elongation and narrowness, easily distinguish *Peramium pubescens*. In *Peramium repens* the cells are shorter, often quite equilateral and intercellular spaces abound. In the species of *Listera* examined the same specific differences exist. In *Listera cordata* is noted a decided departure from *Listera*

australis and *L. convallarioides* in its elongated testa and the squareness of its cells. The relationship of *Listera convallarioides* and *L. australis* is altogether too close. Of *Listera australis* but indifferent specimens were procurable, and the figure may not be typical. It is separated from *convallarioides* by a longer cell and less rotund testa, and the seed indicates that it is in closer relation with *L. cordata* than is *L. convallarioides.*

It may be worthy of note that the seeds often appeared as indicative of the character or disposition of the plant. In the case of *Peramium* the seeds of the two species examined did not always show constant and pronounced features, and there was an obvious tendency to variation, and assumption of characters common to both.

In *Pogonia* the reverse is to be noted. By reference to the figures it will be seen how strongly the individual features of each species are manifested. These pronounced characters indicate a decided bent in the plant life that has made a sharp demarkation of species. And we would expect to find the species widely separated and rigidly fixed, as is the fact. In the case of *Pogonia affinis* and *Pogonia verticillata* no noteworthy difference exists. The form of seed, character of cell, wall and nucellus are identical. It is to be seriously doubted if any tangible distinction can be maintained between these two species. Furthermore such is the disposition of the genus that we would expect pronounced features to characterize the species. It should be said that but one specimen, and that an excellent one, was examined. I would consider it a favor to receive mature fruit of this plant.

In examining these seeds one fact came out very clearly, i. e. the importance of the fruit as one of the prime factors of classification. This would naturally be the case, for the fruit is the consummation of the plant life. In the nucellus rests the occult power to produce its kind; here also is lodged the impetus to change and variation. Climate and soil and cultivation may assist the plant in its departure from the parent type, but that restlessness which renders the classification of some genera so difficult, is due more to the hidden force lodged by the plant in the nucellus than all other combined influences. It seems reasonable, therefore, that something of this inherent disposition of the plant that is to

be, ought to be manifest in the seed and so serve as a truer index to its position and relationship. And this fact, it seems to me, appears with unmistakable clearness in the case of our Eastern Orchids.

Explanation of Plates.

PLATE CL.

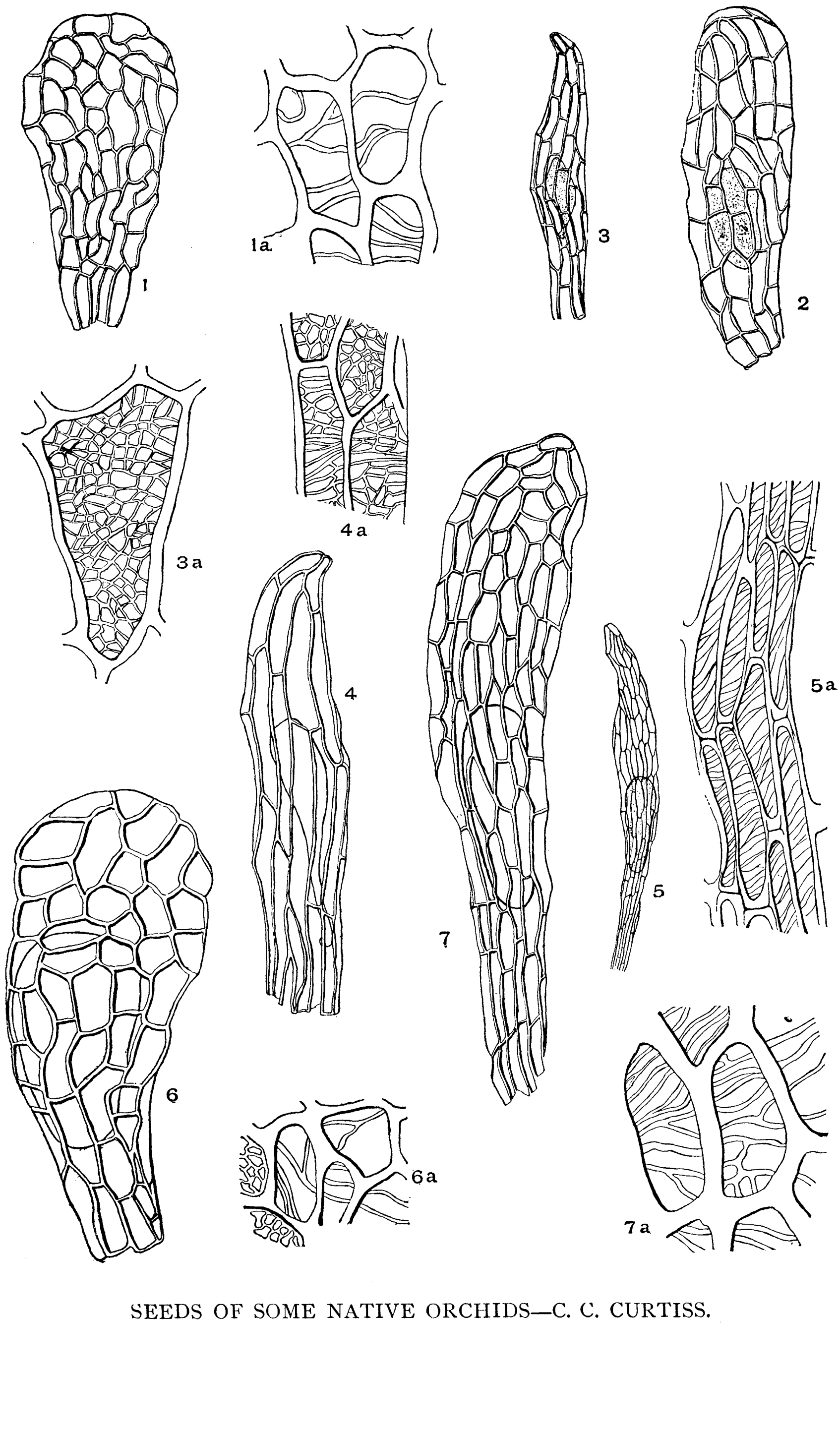
Fig. 1. Testa of *Acroanthes unifolia* × 100.
Fig. 1a. Same showing sculpturing of inner cell wall of testa × 325.
Fig. 2. *Liparis liliifolia*, seed × 100.
Fig. 3. *Calypso bulbosa*, seed × 60.
Fig. 3a. Same showing sculpturing of inner cell wall of testa × 325.
Fig. 4. *Tipularia unifolia*, seed × 100.
Fig. 4a. Same showing sculpturing of inner cell wall of testa × 325.
Fig. 5. *Aplectrum spicatum*, seed × 35.
Fig. 5a. Same showing sculpturing of inner cell wall of testa × 180.
Fig. 6. *Corallorhiza innata*, seed × 125.
Fig. 6a. Same showing sculpturing on inner cell wall of testa × 325.
Fig. 7. *Corallorhiza multiflora*, seed × 115.
Fig. 7a. Same showing sculpturing of inner cell wall of testa × 325.

PLATE CLI.

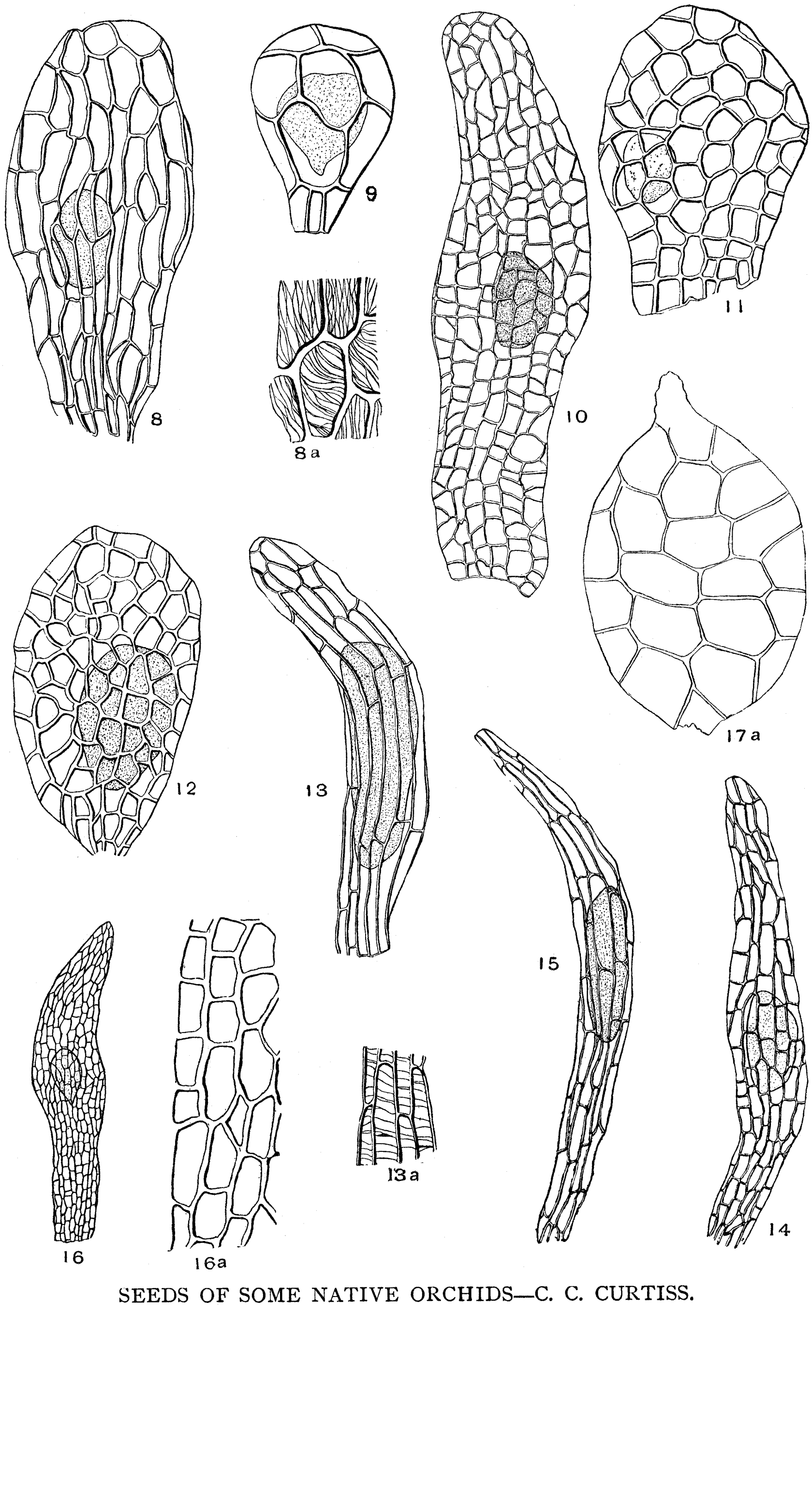
Fig. 8. *Hexalectris aphyllus*, seed × 100.
Fig. 8a. Same showing sculpturing on inner cell wall of testa × 175.
Fig. 9. *Bletia verecunda*, seed × 100.
Fig. 10. *Listera cordata*, seed × 100.
Fig. 11. *Listera australis*, seed × 100.
Fig. 12. *Listera convallarioides*, seed × 100.
Fig. 13. *Gyrostachys cernua*, seed × 120.
Fig. 13a. Same showing the sculpturing on inner cell wall of testa × 175.
Fig. 14. *Peramium repens*, seed × 55.
Fig. 15. *Peramium pubuscens*, seed × 75.
Fig. 16. *Epipactis viridiflora*, seed × 30.
Fig. 16a. Same showing cell wall over nucellus × 200.
Fig. 17a. Nucellus of same showing arragement of cells × 175.

PLATE CLII.

Fig. 17. *Arethusa bulbosa*, seed × 100.
Fig. 18. *Limodorum tuberosum*, seed × 100.
Fig. 19. *Pogonia ophioglossoides*, seed × 55.
Fig. 19a. Same showing sculpturing on inner cell wall of testa × 175.
Fig. 20. *Pogonia trianthophorus*, seed × 100.
Fig. 20a. Same showing sculpturing on inner cell wall of testa × 325.
Fig. 21. *Pogonia verticillata*, seed × 55.
Fig. 22. *Pogonia affinis*, seed × 55.
Fig. 23. *Orchis spectabilis*, seed × 60.
Fig. 24. *Habenaria ciliaris*, seed × 75.
Fig. 25. *Cypripedium pubescens*, seed × 30.
Fig. 25a. Same showing cell wall over nucellus × 100.



SEEDS OF SOME NATIVE ORCHIDS—C. C. CURTISS.



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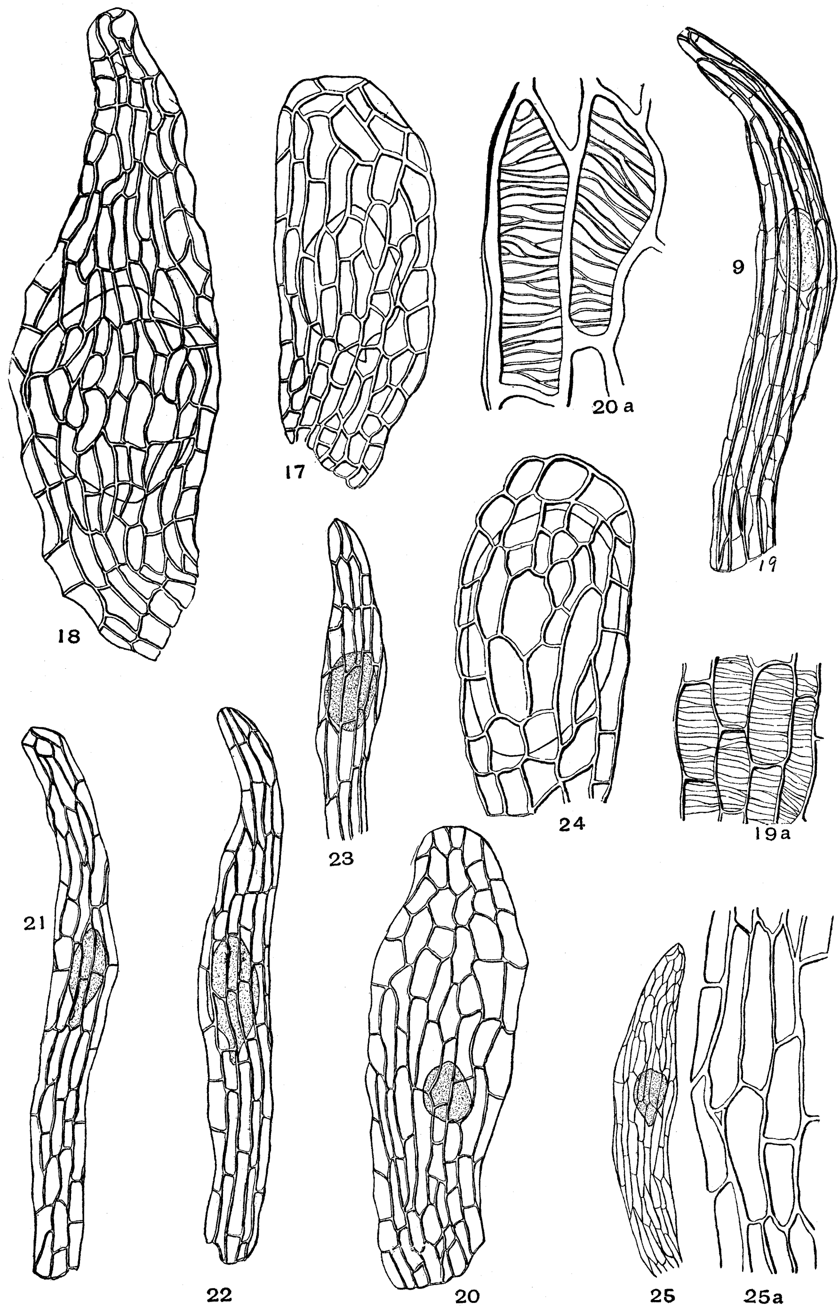

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